

## THE EXTINCT MARSUPIAL GENUS PALORCHESTES OWEN

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As part of a project aiming at a better understanding of the extinct marsupials of Queensland, the specimens in the collections of the Queensland Museum which served as the basis of the work of C. W. De Vis, published towards the close of the last century, are being prepared and restudied. One of the genera studied by De Vis (1884, 1895) was *Palorchestes* Owen and the re-examination of available specimens, together with the relevant literature, has enabled the presentation of results of some taxonomic significance.

Two species are recognised—the type species *P. azael* Owen, originally described on the basis of a cranial fragment from Victoria, and *P. parvus* De Vis, based on specimens from the Darling Downs, Queensland. Both are redescribed. An assessment of the meagre locality data associated with the old collections in the Queensland Museum, in the light of recent field work, has revealed information of possible stratigraphic value.

All measurements are in millimetres.

**PALORCHESTES AZAEL** Owen

(Figures 1–3)

*Palorchestes azael* Owen, 1874, Phil. Trans., pp. 797–800, pl. 81, figs. 1, 2, pl. 82, fig. 1., pl. 83, fig. 1; Owen, 1876, Phil. Trans., pp. 197–199, pls. 19, 20, but not pp. 199–204, pp. 218–220, pl. 21, pl. 22, figs. 1–4, pl. 23, figs. 1, 2, 4, 5, pl. 24, and pl. 29, figs. 1–3; De Vis, 1884, Proc. Linn. Soc. N.S.W., 8, pp. 221–224; Lydekker, 1887, Cat. Foss. Mamm. B.M. (N.H.), pt. 5, pp. 237–238; Dun, 1893, Rec. Geol. Surv. N.S.W., 3, pp. 120–124, pl. 16; De Vis, 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 81–84, pl. 14, figs. 1–6.

*Palorchestes crassus* Owen, 1880, Trans. Zool. Soc. Lond., 11, pp. 7–10, pl. 2.

*Palorchestes* sp. Scott, 1916, Pap. & Proc. Roy. Soc. Tas. for 1915, pp. 100–101, pl. 9.

**MATERIAL.**—Referred specimens in the collections of the Queensland Museum are as follows: F.772, incomplete right maxilla with  $M^{1-2}$ , juvenile, Darling Downs, S.E. Queensland (figd. De Vis, 1895, pl. 14, fig. 3); F.773, cast of palate with cheek teeth, Wellington Caves, New South Wales (figd. in part, De Vis, 1895, pl. 14, figs. 5, 6); F.774, nearly complete mandible with right  $I_1$ ,  $DP_3$ – $M_3$ , left  $I_1$ ,  $M_{1-3}$ , juvenile, near St. Ruth\*, Darling Downs (described De Vis, 1884, figd. in part, De Vis, 1895,

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\* In the later paper De Vis (1895) gives the locality as “Peak Downs.”

pl. 14, figs. 1, 2) ; F.780, left mandibular fragment with  $M_3$ , Darling Downs ; F.781, left mandibular fragment with  $P_3$ - $M_2$ , Darling Downs (figd. in part, De Vis, 1895, pl. 14, fig. 4) ; F.1303, left mandibular fragment with  $M_{2-4}$ , Darling Downs ; F.2203, right  $I_1$ , Condamine River, near Dalby, Darling Downs ; F.2780, left mandibular fragment with  $M_{3-4}$ , Macalister, Darling Downs ; F.2937, right mandibular fragment with  $M_3$ , King Creek, Darling Downs, at 039454 Clifton 1 mile military map.

## Measurements

## Maxilla

Specimen	$P^3$	$M^1$	$M^2$	$M^3$	$M^4$
TYPE, B.M.(N.H.) No. 46316, measured from Owen (1874) pl. 82, fig. 1.	19.3 x	24.1 x 19.6	25.4 x 21.2	25.7 x 20.3	27.1 x 22.7
	—	—	25.1 x 23.0	25.8 x	—
Specimen described by Dun (1893). Lengths from p. 123, breadths measured from pl.16	21.5 x 20.5	27.5 x 23.0	28.5 x 25.0	29.0 x 25.0	—
F. 772 .. .. .	—	27.8 x 23.0	28.8 x 24.3	—	—
F. 773 .. .. .	18.6 x 17.7	26.0 x 22.3	26.5 x 23.2	26.7 x 22.6	28.5 x 21.3
	18.4 x 17.3	26.1 x 21.8	26.8 x 22.7	27.8 x 22.6	27.6 x 22.0

Premaxillae anteriorly wide, thickened in region of implantation of nearly transverse incisor row ; rising steeply to broad, rounded nasal spine ; then separating, diverging slightly, rising less steeply in extensive ventral edge of bony nostril. Palate gradually ascending in extensive diastema between  $I^3$  and  $P^3$  ; slightly constricted anterior to  $P^3$  ; medianly channelled, with anterior palatine foramina apparently confluent, rather posterior. Palate posteriorly widening in region of cheek teeth, posteriorly without vacuities. Anterior root of zygoma almost perpendicular, opposite  $M^2$  and part of  $M^3$  in adult. Maxillae deeply excavated near midline in narial passage, opposite root of zygoma.

$$\text{Dental formula : } I \frac{1.2.3}{1.0.0} \quad C \frac{0}{0} \quad P \frac{0.0.3}{0.0.3} \quad M \frac{1.2.3.4}{1.2.3.4}$$

Upper incisors unknown, but alveoli indicate they form slightly arcuate row, with  $I^1$  the smallest.

Upper cheek teeth in slightly curved rows, diverging posteriorly.  $P^3$  roundly subtriangular, wearing in lower plane than molars ; transversely bicuspid, with large subcentral paracone, sometimes with its crest complex and exhibiting a prominent labial cleft, one or more forelinks, and narrow, rounded anterior cingulum ; protocone also prominent, separated from paracone almost to base by deep valley ; posterior cingulum wide, but low, extending almost across greatest width of tooth ; anterior root narrow, somewhat antero-dorsally directed ; posterior root wide, oblique, extending to above protocone.  $DP^3$  not preserved, but alveolus shows it to be posteriorly bi-rooted, wide.

Molars bilophodont, subequal, with slight increase in length posteriorly, but with progressive decrease in width across metaloph from  $M^2$  to  $M^4$  and corresponding change in outline from subrectangular to subtrapeziform. Molar row showing some forward movement relative to anterior root of zygoma in adult life and mutual attrition of anterior and posterior cingula in adjacent anterior teeth. Loph high, slightly crescentic and oblique when unworn; laterally smooth, convergent; anteriorly and posteriorly with fine irregular ridges and furrows. Anterior cingulum well developed, extending across width of protoloph, strongest in  $M^1$ , stronger lingually in posterior teeth. Forelink strong, multiple in  $M^1$ ; otherwise rather weak, submedian, descending to elevated portion of anterior cingulum. Median valleys deep, V-shaped, with weak labial and stronger lingual cingula. Midlinks high, divided; low accessory lingual midlink in  $M^1$  and  $M^2$  and labial structure in  $M^1$ ; posterior swelling of protocone also helps to constrict lingual part of valley. Hindlink appearing as swelling of hypocone, descending and swinging labially. Posterior cingulum lower and weaker than anterior cingulum, weaker in posterior teeth, stronger labially.

## Measurements

## Mandible

Specimen	DP <sub>3</sub>	P <sub>3</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>	Depth of ramus below M <sub>3</sub>
B.M. (N.H.) No. 40034, measured from Owen (1876) pl. 19.	{ —	—	22.7 x 16.1	27.1 x 17.8	29.4 x 20.0	—	72 (aged)
—		—	—	26.9 x 18.1	—	—	
B.M. (N.H.). No. 34, type of <i>P. crassus</i> , meas- ured from Owen (1880) pl. 2.	—	—	—	26.9 x	33.0 x	29.5 x	74 (aged)
F. 774 .. ..	{ 12.2 x 7.8	18.5 x	23.4 x 14.7	28.5 x 17.7	27.6 x	—	36 (juvenile)
.. ..		—	22.4 x 13.3	28.2 x 17.7	27.2 x	—	
F. 780 .. ..	—	—	—	—	29.7 x 17.9	—	61 (aged)
F. 781 .. ..	—	17.4 x 10.4	23.7 x 15.6	27.2 x 17.0	—	—	56 (aged)
F. 1303 .. ..	—	—	—	22.4 x 15.9	23.7 x 16.3	24.1 x 16.2	44 (adult)
F. 2780 .. ..	—	—	—	—	25.0 x 16.3	26.4 x 16.5	57 (aged)
F. 2937 .. ..	—	—	—	—	26.2 x 16.4	—	53 (aged)

Mandible descending anteriorly; symphysis elongate, rami moderately firmly united but not ankylosed in juvenile. Symphyseal region dorsally excavated, V-shaped behind, becoming shallow and broadly U-shaped anteriorly; postero-ventrally carinate. Diastema extensive, diastemal crest descending sharply anterior to premolar. Mental foramen antero-ventral to premolar. Diagastric process rather weak, separated by shallow postdiagastric sulcus from base

of angle; wall of ramus above process shallowly concave, opening posteriorly into deeper pterygoid fossa; mesial margin of fossa thickened. Postalveolar shelf elongate triangular, passing to postalveolar ridge leading to large dental foramen. Masseteric fossa shallow, ridged; masseteric foramen absent.

$I_1$  broad, spoon-shaped, of thin section; approximated at tips, with development of mesial facet of wear; surface of wear with upper incisors broadly arcuate, whole labial margin subhorizontal; enamel thin, finely and irregularly ridged, laterally with low sharp dorsal flange.

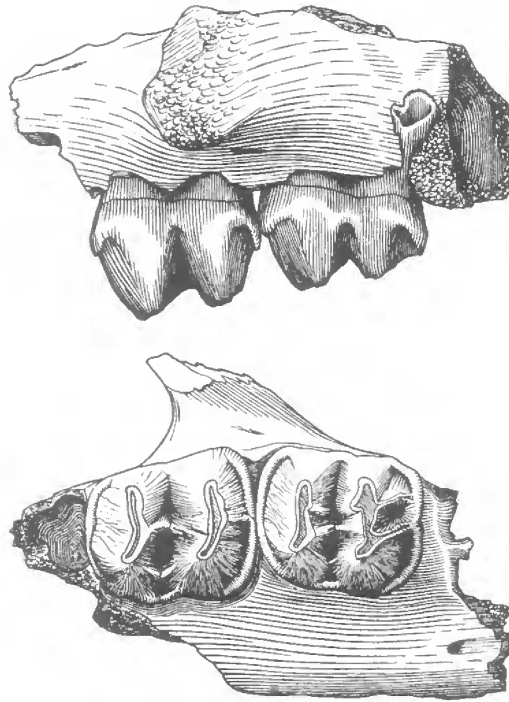


Figure 1.—*Palorchestes azeel* Owen. Lateral and occlusal views of maxillary fragment; F. 772, three-fourths natural size.

Lower cheek teeth in straight rows, divergent posteriorly.  $DP_3$  relatively small, elongate ovate, unequally bilophodont; protolophid relatively narrow in worn condition, with prominent labial forelink, descending slightly and curving antero-lingually to join short high anterior cingulum, discontinuous lingually; midlink divided, nearly labial, posteriorly joining weak hypoconid on reduced cingulum-like hypolophid. Eruption of  $P_3$  beginning after that of  $M_4$ .  $P_3$  ovate, with single high subcentral cusp wearing in lower plane than molars; forelink short, labial, steeply descending to elevated part of narrow anterior cingulum; posterior link descending, crossing the talonid basin medianly, with slight posterior expansion immediately dorsal to elevated median portion of arcuate posterior cingulum; short accessory link descending posteriorly from main cusp, partially closing talonid valley lingually;  $P_3$  birooted, roots divergent, posterior root stronger.

Lower molars subrectangular, slightly constricted in region of median valley.  $M_1$  considerably shorter than others; size relationship of others variable. Molar row showing some forward movement in adult life, with mutual attrition of anterior and posterior cingula in adjacent anterior teeth and progressive change in attitude of roots of posterior molars. Lophids high, crescentic and oblique when unworn; laterally smooth, only slightly convergent; anteriorly and posteriorly with fine irregular ridges and furrows. Anterior cingulum most conspicuous in  $M_1$ , otherwise stronger lingually; forelink broadly rounded, stemming from protoconid, stronger in posterior molars. Median valley deeply V-shaped, with labial cingulum and styloid of variable development, and occasionally weaker indication of lingual cingulum; midlink high, divided, anterior part arising from near middle of protolophid, longer posterior part from hypoconid; low accessory lingual midlink in  $M_1$  and  $M_2$ , variable. Hindlink lower than midlink, descending from near middle of hypolophid to sharply elevated middle portion of strong posterior cingulum.

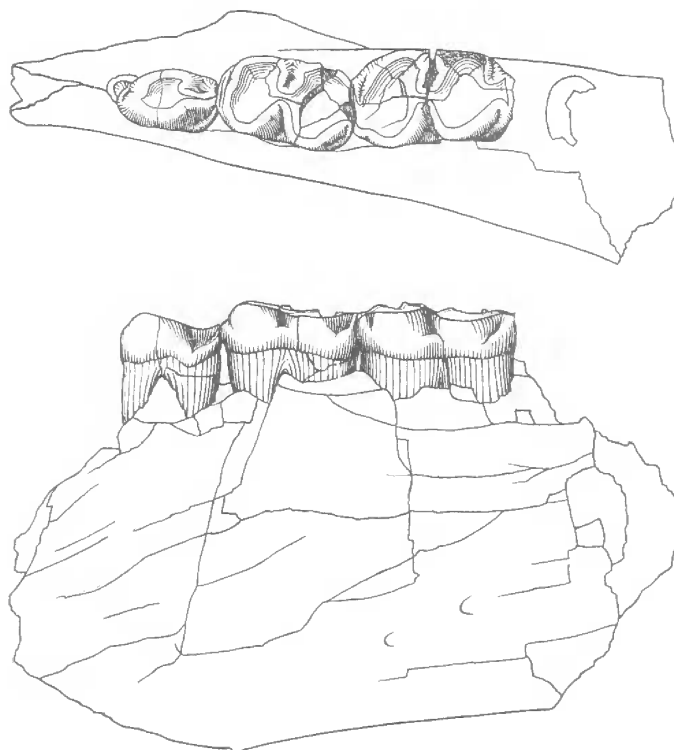


Figure 2.—*Palorchestes azael* Owen. Occlusal and lateral views of mandibular fragment; F. 781, three-fourths natural size.

While there is no record of the field association of cranial and mandibular remains, the latter are referred to the species with certainty. The development of the midlinks is similar in upper and lower molars, and occlusion is satisfactory. The same cannot be said of the relationship of the postcranial remains—innominate bone, sacrum, femur, tibia, calcaneum, and metatarsals—referred by Owen (1876) to this

species. There is again no record of field association with skull remains, and the comparative morphology of the postcranial skeleton of the large extinct phalangeroid marsupials is too poorly known for valid specific or even generic determination of isolated bones. Furthermore the postcranial fossils assigned by Owen to the species reflect his ideas of the systematic position of the genus which are later (p. 190) shown to be erroneous. Additional postcranial fossils, referred to *P. azael*, in the collections of the Australian Museum, Sydney, were mentioned by Fletcher (1945). Mr. H. O. Fletcher has informed me that these specimens were identified by the late Dr. Charles Anderson. In the absence of established field association their identity must remain doubtful.

Gregory (1902) tentatively referred a lower incisor and associated postcranial remains from the dune sandstone at Fowler's Cove, Nepean Peninsula, Victoria, to this species. The tooth, which is in the collections of the National Museum of Victoria (reg. No. P7419), has been kindly made available for examination by the Director, Mr. C. W. Brazenor. It is a fragment of a right  $I_1$ , of characteristic macropodid aspect, and is referable to one of the extinct species of *Protemnodon* Owen of large individuals.

The juvenile mandible (fig. 3) shows pronounced dextral curvature in occlusal view. The specimen shows postmortem fractures, but as there is no lateral displacement along these fractures, the asymmetry cannot be satisfactorily interpreted as postdepositional strain. Apparently it is an example of parameral differentiation, which in marsupials has been previously described for the living wombat *Lasiorhinus latifrons barnardi* Longman by Tucker (1954).

As indicated in the accompanying tables of measurements, cheek teeth in *P. azael* vary considerably in size and proportions. The progressive obliteration of the anterior and posterior cingula, resulting from crowding of the molars in aged individuals, is a contributing factor. However, teeth may vary in the same skull, as strikingly illustrated by the right and left  $P^3$  in the specimen described and figured by Dun (1893).

Lydekker (1887) relegated *P. crassus* to synonymy with *P. azael*. He claimed that the anomalous condition of the molars of the right ramus described and figured as the type were not repeated in the left ramus of the same specimen (which Owen did not mention). In support of Lydekker's argument it may be pointed out that it is apparent from Owen's figures (1880, pl.2) that distortion of the right ramus, involving postmortem fracturing, expansion, and cementation with matrix has occurred, especially in the region of  $M_3$  ( $M_2$  of Owen), and this factor, which is, of course, superimposed on the natural intraspecific variation, must be considered in the taxonomic evaluation of apparent anomalies in the size relationships of the molars.

The abnormally large  $M_2$  in F.774 (Q.M.) has also been subjected to postmortem fracture and expansion. The strong development of the labial cingulum in the type of *P. crassus* is not considered significant. Specimens of *P. azael* have this structure variably developed, but on the whole more strongly in large individuals.

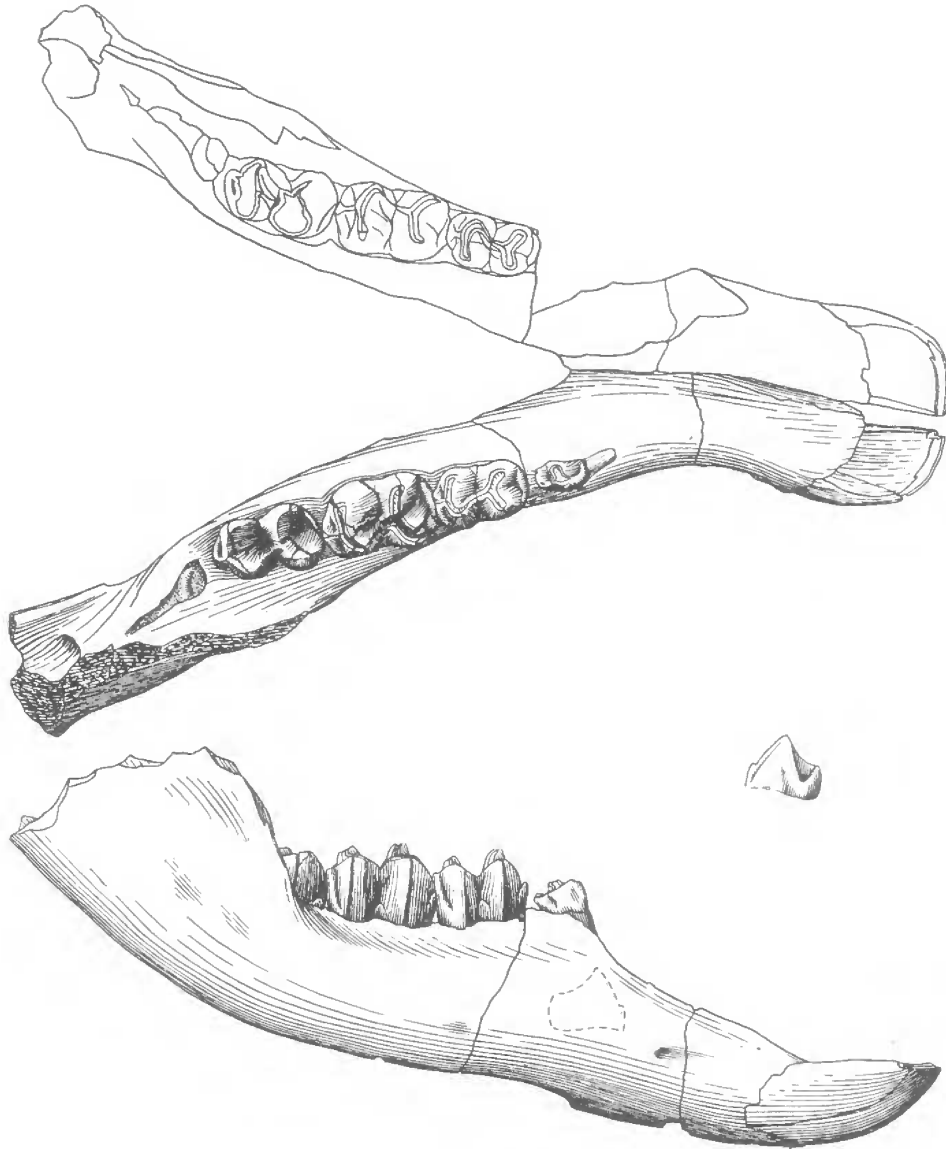


Figure 3.—*Palorchestes azael* Owen. Occlusal and lateral views of juvenile mandible, and lingual view of unerupted  $P_3$  exposed by fenestration of the ramus. The position of this tooth is indicated by the broken line; F. 774, half natural size.

Tate (1948) questioned the identity of *P. crassus* with *P. azael* on account of the apparent disparity in the lengths of the diastemata of the type material. However, the mandibular symphysis is elongate in *P. azael* (fig. 3) and the type ramus of *P. crassus* is obviously very incomplete anteriorly.

The specimen from Mowbray Swamp, Smithton, Tasmania, described and figured by Scott (1916) as *Palorchestes* sp., consists of a maxillary fragment with P<sup>3</sup>-M<sup>2</sup> and portion of M<sup>3</sup>. Its size and configuration indicate that it can be referred to *P. azael*.

While fossils of *P. azael* are not common, they are widely distributed in Eastern Australia in deposits believed to be of Pleistocene age. There is also a record of the species from the Margaret River Caves, S.W. Western Australia, by Glauert (1926).

Hall and Pritchard (1897), on the basis of an identification by De Vis, referred an upper premolar from the Upper Miocene marine beds of Beaumaris, Victoria, to *Palorchestes*. As Stirton (1957) has indicated, this tooth may be referred to the Diprotodontidae; it resembles P<sup>3</sup> described for species of *Nototherium* Owen.

Fragments of two molars, mainly alveolar, from Castle Creek, Rannes, Mid-east Queensland, were referred by Longman (1929) to *Palorchestes* sp., but regarded as inadequate for precise determination. These fragments have not been located in the Queensland Museum collections.

#### PALORCHESTES PARVUS De Vis

(Figures 4, 5)

*Palorchestes parvus* De Vis, 1895, Proc. Linn. Soc. N.S.W., 10 (n.s.), pp. 84-88, pl. 14, figs. 7-10.

**MATERIAL.**—The type was not designated by De Vis, and F.783, a left mandibular fragment with P<sub>3</sub>-M<sub>4</sub> well preserved, Darling Downs, S.E. Queensland (figd. De Vis, 1895, pl.14, fig. 9) is chosen as the lectotype.

F.778, right M<sup>3</sup>, Darling Downs; F.784, left M<sup>1</sup>, Darling Downs (figd. De Vis, 1895, pl.14, fig. 7); F.789, fragments of premaxillae, maxillae, right jugal and squamosal, with complete dentition except left P<sup>3</sup>, aged, Darling Downs (figd. in part, De Vis, 1895, pl.14, figs. 8, 10); F.2966, right maxillary fragment with M<sup>2-3</sup>, Chinchilla, Darling Downs; F.2967, left maxillary fragment with M<sup>1-3</sup>, Darling Downs; F.2968, right maxillary fragment with M<sup>1-2</sup>, Chinchilla, Darling Downs; F.3299, left maxillary fragment with M<sup>2</sup>, Darling Downs; F.786, left mandibular fragment with M<sub>1-4</sub>, Chinchilla, Darling Downs; F.793, left mandibular fragment with M<sub>2-4</sub>, Chinchilla, Darling Downs; F.2969 right mandibular fragment with M<sub>3-4</sub>, Darling Downs; F.3300, left mandibular fragment with M<sub>2-4</sub>, Darling Downs; F.3301, right mandibular fragment with M<sub>3</sub>, Darling Downs.



## Measurements

## Maxilla

Specimen	P <sup>3</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	M <sup>4</sup>
F. 778 .. .. .	—	—	—	22.3 x 17.5	—
F. 784 .. .. .	—	22.1 x 17.3	—	—	—
F. 789 .. .. .	16.8 x 14.5	18.8 x 14.7	20.3 x 16.1	21.2 x 16.3	24.0 x 16.7
		17.8 x 14.2	20.6 x 16.2	21.3 x 16.5	23.3 x 16.6
F. 2966 .. .. .	—	—	20.1 x 17.1	19.6 x 16.6	—
F. 2967 .. .. .	—	20.1 x 15.8	19.9 x 16.1	20.8 x 15.9	—
F. 2968 .. .. .	—	19.3 x 15.5	18.7 x 15.0	—	—
F. 3299 .. .. .	—	—	21.1 x 17.5	—	—

Premaxillae anteriorly wide, rather flattened; rising medianly to broad, nearly vertical nasal spine; then separating, deeply but asymmetrically excavated dorsally; rising posteriorly as thin strip capping maxilla and forming extensive ventral edge of bony nostril. Anterior root of zygoma nearly perpendicular, with indication of ventro-lateral process involving thickening of both maxilla and jugal; pierced by short infraorbital canal opening at foramen above anterior root of M<sup>2</sup>. Jugal exceeding maxilla in nearly straight lateral part of arch; not excavated laterally for superficial layer of masseter; glenoid fossa narrow, bearing surface flat, restricted to jugal.

Upper incisors I<sup>1</sup> < I<sup>2</sup> < I<sup>3</sup>; roots expanding from alveoli, curving and converging so crowns are contiguous at their working surface. Surfaces of wear forming nearly transverse arch; enamel only labially in worn teeth, rather thin; that of I<sup>2</sup> with shallow median cleft.

Upper cheek teeth in slightly curved rows diverging slightly posteriorly. P<sup>3</sup> large, roundly subtriangular, wearing in lower plane than molars; transversely bicuspid; with large subcentral paracone, short labial forelink, descending to rounded antero-lingual cingulum, prominent posterior link descending to join elevated submedian portion of wide curved posterior cingulum; protocone also prominent, separated from paracone almost to base by deep valley; joined to anterior and posterior cingula; anterior root narrow; posterior root wide, oblique, extending to above protocone.

Molars bilophodont, first three subequal in length in unworn condition, M<sup>4</sup> longer; progressive decrease in width across metaloph from M<sup>2</sup> to M<sup>4</sup> and corresponding change in outline from subrectangular to subtrapeziform. Molar row showing some forward movement relative to anterior root of zygoma in adult life, and mutual attrition of anterior and posterior cingula on adjacent anterior teeth. Loph high, slightly crescentic and oblique when unworn; laterally smooth, convergent; anteriorly and posteriorly with ridges and furrows variably developed. Anterior cingulum strong in anterior teeth, extending across width of protoloph; weaker posteriorly, stronger there lingually. Forelink strong, double in M<sup>1</sup>, otherwise becoming progressively weaker;

on labial side of midline. Median valleys deep, V-shaped, with weak labial and stronger lingual cingula, variably developed. Midlinks high, divided, double in  $M^1$ , posterior part progressively stronger in posterior teeth. Hindlink double in  $M^1$ , otherwise appearing as posterior inflation of hypocone. Posterior cingulum weaker than anterior cingulum; weaker in posterior teeth, stronger there labially. Roots becoming exposed with age; anterior root divided.

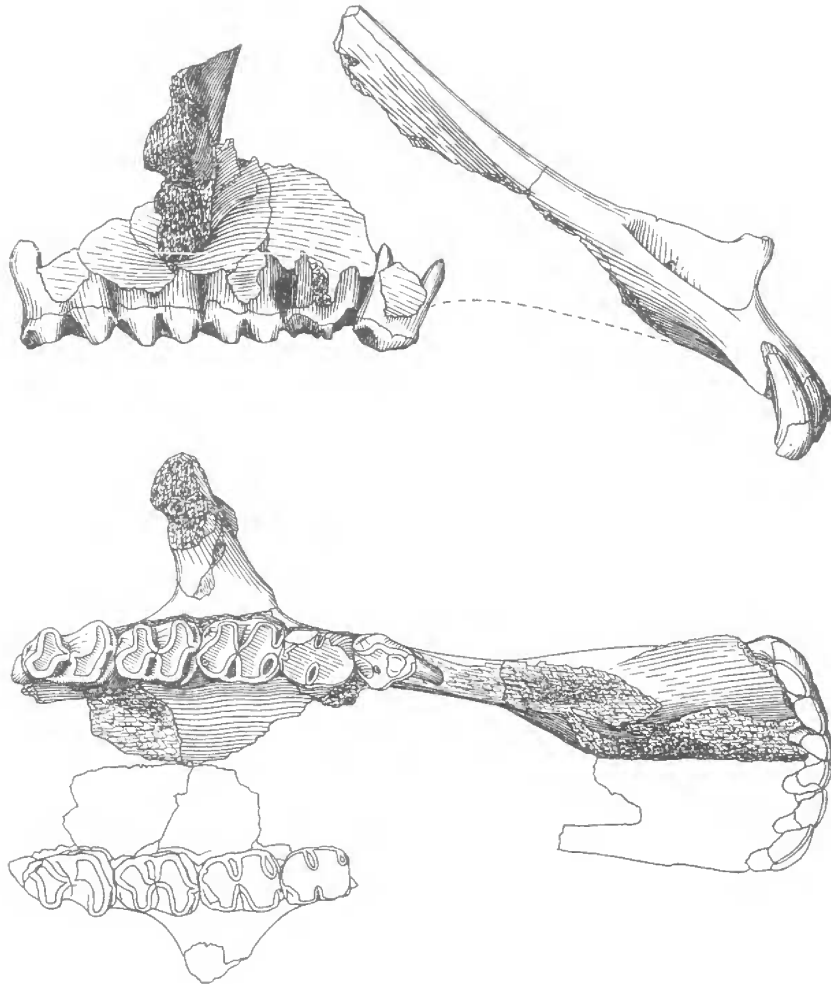


Figure 4.—*Palorchestes parvus* De Vis. Lateral and occlusal view of cranial fragments; F. 789, half natural size.

## Measurements

## Mandible

Specimen	P <sub>3</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	M <sub>4</sub>	Depth of ramus below M <sub>3</sub>
F. 783 (type) ..	14.9 x 10.6	19.7 x 12.3	20.6 x 12.6	20.8 x 12.8	20.6 x 13.1	37
F. 786 .. ..	—	—	20.8 x 13.7	21.1 x 14.1	22.0 x	49
F. 793 .. ..	—	—	19.2 x 11.1	21.0 x 12.3	20.0 x 12.4	42
F. 2969 ..	—	—	—	21.0 x 14.6	21.0 x 13.9	50
F. 3300 ..	—	—	19.1 x 11.8	19.8 x	19.1 x 12.2	39
F. 3301 ..	—	—	—	19.4 x 12.1	—	36

Mandible deepest in posterior symphyseal region below P<sub>3</sub> and M<sub>1</sub>. Lower border of ramus nearly straight between symphysis and diagastric process, then ascending at low angle; diagastric process rather weak, separated by shallow postdiagastric sulcus from base of angle; wall of ramus above process shallowly concave, opening posteriorly into deeper pterygoid fossa; mesial margin of fossa thickened. Postalveolar shelf narrow, passing to well-defined, subhorizontal but flexed postalveolar ridge leading to large dental foramen. Outer wall of ramus nearly vertical in alveolar region, exhibiting interrootal depressions; laterally convex, with convexity increasing markedly towards emergence of coronoid process; anterior margin of process reclined beyond vertical at base. Masseteric fossa shallow, ridged; masseteric foramen absent.

Lower cheek-teeth in a straight row. P<sub>3</sub> large, elongate, roundly subtriangular; with single high subcentral cusp, wearing in lower plane than molars to obliquely transverse lophid-like structure; forelink short, labial, descending steeply to narrow antero-lingual cingulum; also short steep lingual accessory forelink; posterior link divided, curved, crossing talonid basin labially; joining low lophid-like structure, standing above middle portion of extensive curved posterior cingulum; short accessory link descending posteriorly from main cusp, partially closing talonid valley lingually.

Molars subrectangular, slightly constricted in region of median valley; increasing posteriorly in length to M<sub>3</sub>, with M<sub>4</sub> subequal to it. Molar row showing some forward movement in adult life, with mutual attrition of anterior and posterior cingula in adjacent anterior teeth. Lophids high, crescentic and slightly oblique when unworn; laterally smooth, slightly convergent; unworn parts of valleys finely ridged, punctate; protolophid and hypolophid subequal in anterior molars; hypolophid markedly narrower in M<sub>4</sub>. Enamel thicker in posterior teeth. Anterior cingulum short; weak or absent labially in posterior teeth. Forelink stronger in posterior molars, stemming from protoconid, descending and swinging mesiad. Median valley deeply V-shaped, with labial cingulum and low stylid of variable development, chiefly in M<sub>2</sub>; midlink high, divided; anterior portion derived from near middle of protolophid, longer posterior part from hypoconid. Hindlink descending from near middle of hypolophid to sharply elevated middle portion of strong posterior cingulum; link and cingulum not so well developed in M<sub>4</sub>.

The skull remains suggest that individuals of *P. parvus* were smaller and more lightly built than those of *P. azael*. The dentition in *P. parvus* generally resembles that of *P. azael* but differs in details; notably the upper and lower third premolars are larger, relative to the molars; the upper molars are relatively narrower and the hindlink of  $M^1$  is more complex; the lower molars have lower midlinks. The range in variation of crown dimensions in each species is considerable, but there is no overlap. The premaxillae are anteriorly less robust in *P. parvus* than in *P. azael*.

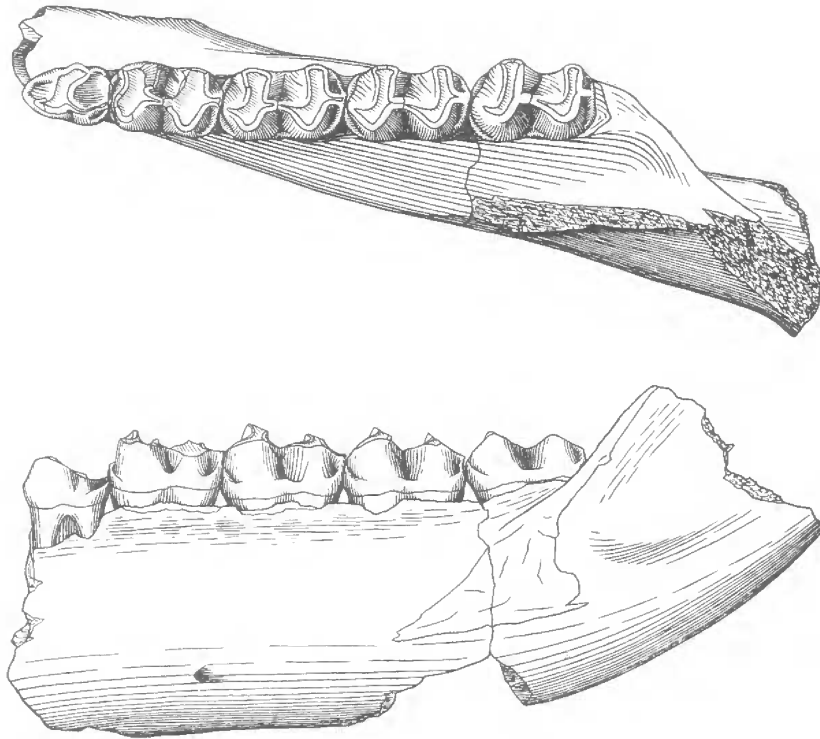


Figure 5.—*Palorchestes parvus* De Vis. Occlusal and lateral views of incomplete ramus; F. 783, type, three-fourths natural size.

Their free extension postero-dorsally suggests that in the lateral excavation of the bony nostril *Palorchestes* may have paralleled some of the Pliocene equid genera such as *Hippidion*. It is not known whether the maxilla contributed to the edge of the bony nostril; Owen's (1874) description and figures of *P. azael* indicate it as a possibility, but the cranium of *P. parvus* (fig. 4) is incomplete in the critical region. The function of the prominent asymmetric dorsal excavations of the premaxillae in the latter specimen is unknown. They have no counterpart in the type cranium of *P. azael* unless it is the narrow oblique cavity behind the alveolus of  $I^3$  on the right side, which Owen (1874) suggested may have been the alveolus of a rudimentary

canine. However, its lateral position and its distance from the premaxillo-maxillar suture makes its interpretation as an alveolus improbable. There is certainly no apparent evidence for Tate's (1948) statement that "there is a rather large upper canine."

Apart from some imperfect teeth from Smithton, Tasmania, which were not described and figured, but were provisionally referred by Scott and Lord (1925) to *P. parvus*, this species is recorded only from the Darling Downs, Queensland. Of the thirteen specimens referred to in this paper only four have a more precise locality and in all cases this is "Chinchilla." Most of the old collections of fossil marsupials in the Queensland Museum were obtained by K. Broadbent and H. Hurst about 70 years ago. Current field work suggest that their locality "Chinchilla" refers to an area embracing banks of the Condamine River and adjacent gullies, some three or four miles south-east of the present town. *P. azael* has not been recorded in this area but it is known from localities further east on the Darling Downs between Macalister and Pilton. The suggestion has already been made (Woods, 1956) that the fossiliferous sediments near Chinchilla are older than those farther east and south-east on the Darling Downs and may be Pliocene, and the occurrence of different species of *Palorchestes* in areas of such close proximity is added palaeontological evidence for their stratigraphic distinction. Furthermore, it appears that the dominant diprotodontid element in the Chinchilla fauna was *Euryzygoma dunense* (De Vis) while that of the superficial fluviatile deposits of the eastern Downs was the widely distributed *Diprotodon optatum* Owen. If the suggested age relationship between *P. parvus* and *P. azael* can be established it will be another case of the dominance of giant forms in the Pleistocene.

#### THE SYSTEMATIC POSITION OF THE GENUS

Owen placed *Palorchestes* in the family Macropodidae. This designation has never been questioned, and latterly the genus has been referred to the subfamily Macropodinae by Simpson (1945), and to the subfamily Sthenurinae by Raven and Gregory (1946); while Tate (1948) has placed it in a new subfamily, the Palorchestinae. In the absence of any definite postcranial remains the systematic position of the genus will have to be considered solely on the basis of the skull, which is itself imperfectly known. Three structures stand out as useful in determining the relationship of the genus. They are (a) the masseteric fossa, (b) the dentition, and (c) the zygomatic arch.

##### (a) The Masseteric Fossa.

Abbie (1939) has shown that in the Macropodidae the masseteric fossa is deeply excavated and antero-ventrally invades the body of the ramus. The masseteric foramen is represented by the confluence of this masseteric canal and the

inferior dental canal. Both foramen and canal are absent and the fossa is shallow in *Palorchestes*. In these respects the genus resembles all Diprotodontidae, some Phalangeridae, but none of the Macropodidae. I have checked these structures in *Diprotodon optatum* Owen, *Nototherium mitchelli* Owen, *Euowenia grata* De Vis, *Euryzygoma dunense* (De Vis), and *Meniscolophus mawsoni* Stirton.

(b) The Dentition.

The dental formula for the Macropodidae is  $I \frac{1.2.3}{1.2(0).0} C \frac{1(0)}{0} P \frac{0.2.3}{0.2.3} M \frac{1.2.3.4}{1.2.3.4}$ ; for the Diprotodontidae  $I \frac{1.2.3(0)}{1.0.0} C \frac{0}{0} P \frac{0.0.3}{0.0.3} M \frac{1.2.3.4}{1.2.3.4}$ ; and for the Phalangeridae  $I \frac{1.2.3}{1.2.(0).3.(0)} C \frac{1}{0} P \frac{1.(0).2(0).3}{1.(0).2(0).3} M \frac{1.2.3.4(0)}{1.2.3.4(0)}$ .

The formula for *Palorchestes* agrees with that for the Diprotodontidae. The structure of the cheek teeth may be compared with those of the Diprotodontidae rather than the Phalangeridae or Macropodidae. The single premolar is designated  $P_3^3$  since it has a postfoetal deciduous predecessor and may be regarded as the homologue of the posterior premolar in those marsupials exhibiting the maximum number, and in deference to the arguments of Wilson and Hill (1897) these are designated simply in their order of occurrence in the tooth row. The alternative terminology is that of Thomas (1888) who postulated that the third premolar in modern marsupials is the homologue of  $P_4^4$  of other mammals and designated the tooth accordingly.

$P_3^3$  do not resemble those of *Sthenurus* as commonly claimed (initially by Lydekker, 1887).  $P_3^3$  in outline and ornament generally resembles that of *Euryzygoma dunense* but the cusps are more deeply separated. This tooth in the Diprotodontidae as a whole displays incipient molarization. In the arrangement of the cusps the tooth displays dominantly transverse differentiation as opposed to the dominant longitudinal differentiation, in the development of a longitudinal sectorial edge, in the Macropodidae. The molarization of  $P_3$  in the Diprotodontidae is most striking in *Diprotodon optatum*, where the tooth is quite bilophodont. This is the tooth figured as  $D_3$  by Owen (1877, pl.124). The pattern of the tooth in other genera of the family involves a prominent subcentral cusp, and a prominent wide posterior cingulum.  $P_3$  in *Palorchestes* conforms to this and there is also weak development of a posterior lophid above the cingulum. Of the deciduous premolars only  $DP^3$  has been recorded in the Diprotodontidae and that in the example of *Nototherium mitchelli* described by Glauert (1921). In Diprotodontidae with heavy lower incisors  $P_3$  must be erupted early since the unerupted expanding portion of the crown of  $I_1$  occupies most of the anterior body of the juvenile ramus and the diastema is short at that stage. If  $DP_3$  is erupted at all in such genera it could be expected to be small, not functional, and lost at a very early age. In *Palorchestes azael*  $DP_3$  is a relatively small tooth; more molariform than  $P_3$ . From the size of the alveolus it is obvious that  $DP^3$  was much larger.

The resemblance in dental pattern between that of *Palorchestes* and genera of the Diprotodontidae is maintained in the molars. Owen (1876) compared the molars with those of *Nototherium* and *Diprotodon* in the development of fine rugae and punctations. The most striking diagnostic feature in the molars is the prominence of the posterior cingulum in the lower teeth. In the Diprotodontidae the anterior and posterior cingula are subequal while in the Macropodidae the posterior cingulum is weak or absent and, in contrast, the anterior cingulum is strongly developed.

While the structure of the incisors is variable in the Diprotodontidae that in *Palorchestes* cannot be compared with any genus in the family. These teeth in *Palorchestes* show a specialization for grazing, and the complexity of molar pattern, with the extensive developments of links, supports the view. On the other hand, structural resemblance to the incisors of Macropodidae, even grazing forms, is not close.

In its aggregate the dental evidence shows that *Palorchestes* must be regarded as an aberrant genus of the dominantly browsing Diprotodontidae. This association suggests a rough parallel between adaptive radiation in the Diprotodontidae and that in the Rhinocertoidea of the Eutheria.

(c) The Zygomatic Arch.

While the structure is imperfectly preserved and cannot be considered of equal significance to those previously considered, lack of excavation of the jugal laterally for the superficial layer of the masseter, the lack of outward curvature of this part of the arch, the indication of a broken base of an inferior lateral process involving both jugal and maxilla, and the near perpendicularity of the anterior root of the zygoma are in keeping with the association of *Palorchestes* with the Diprotodontidae.

#### SUMMARY

Two species of *Palorchestes* are recognised—*P. azael* widespread in deposits believed to be Pleistocene, and *P. parvus* known only from deposits near Chinchilla, S.E. Queensland, believed to be older, possibly Pliocene.

From an analysis of the structure of the skull the genus is considered to belong to family Diprotodontidae. Individuals were relatively small, probably lightly built diprotodontids, specialized for grazing.

## LITERATURE CITED

- Abbie, A. A., 1939. A Masticatory Adaptation peculiar to some Diprotodont Marsupials. Proc. Zool. Soc. Lond., Ser. B, 109, pp. 261-279.
- De Vis, C. W., 1884. Notes on a lower jaw of *Palorchestes azael*. Proc. Linn. Soc. N.S.W., 8, pp. 221-224.
- , 1895. A review of the fossil jaws of the Macropodidae in the Queensland Museum. Proc. Linn. Soc., 10 (ser. 2), pp. 75-134, pls. 14-18.
- Dun, W. S., 1893. On Palatal Remains of *Palorchestes azael*, Owen, from the Wellington Caves Bone-deposit. Rec. Geol. Surv. N.S.W., 3, pp. 120-124, pl. 16.
- Fletcher, H. O., 1945. *Palorchestes*—Australia's Extinct Giant Kangaroo. Aust. Mus. Mag., 8, pp. 361-365.
- Glauert, L., 1921. Notes on the Teeth of *Nototherium mitchelli*. Jour. Roy. Soc. W. Aust., 7, pp. 108-111.
- , 1926. A List of Western Australian Fossils (systematically arranged). Supplement No. 1, Bull. Geol. Surv. W.A., No. 88, pp. 36-72.
- Gregory, J. W., 1902. Some remains of an extinct Kangaroo in the Dune-Rock of the Sorrento Peninsula, Victoria. Proc. Roy. Soc. Vict., 14 (n.s.), pp. 139-144.
- Hall, T. S. and Pritchard, G. B., 1897. Note on a Tooth of *Palorchestes* from Beaumaris. Proc. Roy. Soc. Vict., 10 (n.s.), pp. 57-59.
- Longman, H. A., 1929. Palaeontological Notes. Mem. Qld. Mus., 9, pp. 247-252.
- Lydekker, R., 1887. Catalogue of the Fossil Mammalia in the British Museum (Natural History). Pt. 5. London, Taylor and Francis, pp. XVI + 345.
- Owen, R., 1874. On the Fossil Mammals of Australia.—Part IX. Phil. Trans., 164, pp. 783-803, pls. 76-83.
- , 1876. On the Fossil Mammals of Australia—Part X. Phil. Trans., 166, pp. 197-226, pls. 19-31.
- , 1877. Researches on the Fossil Remains of the Extinct Mammals of Australia. London, J. Erxleben, 2 vols., pp. i-XV + 522, pls. 1-131.
- , 1880. Description of a Portion of Mandible and Teeth of a large extinct Kangaroo (*Palorchestes crassus*, Ow.) from ancient fluviatile Drift, Queensland. Trans. Zool. Soc. Lond., 11, pp. 7-10, pl. 2.
- Raven, H. C., and Gregory, W. K., 1946. Adaptive Branching of the Kangaroo Family in Relation to Habitat. Amer. Mus. Nov., No. 1309, pp. 1-33.
- Scott, H. H., 1916. A Note on "*Palorchestes*," as a Tasmanian Pleistocene Genus. Pap. & Proc. Roy. Soc. Tasm. for 1915, pp. 100-101, pl. 9.
- and Lord, C. E., 1925. On Certain Tasmanian Pleistocene Marsupials. Pap. & Proc. Roy. Soc. Tasm. for 1924, pp. 53-58.



- Simpson, G. G., 1945. The Principles of Classification and a Classification of Mammals. Bull. Amer. Nat. Hist., 85, pp. 1-350.
- Stirton, R. A., 1957. Tertiary Marsupials from Victoria, Australia. Mem. Nat. Mus. Viet., No. 21, pp. 121-134.
- Tate, G. H. H., 1948. Results of the Archbold Expeditions. No. 59. Studies on the Anatomy and Phylogeny of the Macropodidae (Marsupialia). Bull. Amer. Mus. Nat. Hist., 91, pp. 235-351.
- Thomas, O., 1888. On the Homologies and Succession of the Teeth in the Dasyuridae, with an Attempt to trace the History of the Evolution of Mammalian Teeth in General. Phil. Trans., 178, pp. 443-462, pls. 27-28.
- Tucker, R., 1954. Pronounced Parameral Differentiation in the Wombat (*Lasiorchinus*). Proc. Roy. Soc. Qd., 65, pp. 71-74, pl. 12.
- Wilson, J. T., and Hill, J. P., 1897. Observations upon the Development and Succession of the Teeth in *Perameles*; together with a Contribution to the Discussion of the Homologies of the Teeth of Marsupial Animals. Jour. Micr. Sci., 39 (n.s.), pp. 427-588, pls. 25-32.
- Woods, J. T., 1956. The Skull of *Thylacoleo carnifex*. Mem. Qld. Mus., 13, pp. 125-140.